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Sound Production and Its Evolutionary Significance in the Blattaria¹

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ABSTRACT

Cockroaches produce sounds by rubbing the abdomen against the wings, tapping the substrate, striking the wings against the abdomen, expelling air through the spiracles, and scraping the pronotum over the costal veins (stridulation). Some of these sounds are made by both sexes when the insects are "disturbed" or by males when they court. Two methods of sound production, namely, stridulation and expulsion of air through the second abdominal spiracles, have evolved in the Oxyhaloinae. Stridulating structures have been found in several genera of the ovoviparous Oxyhaloinae (*Nauphoeta*, *Leucophaea*, *Henschoudetenia*, *Oxyhaloa*, *Jagrehnia*) and 1 genus of Panchlorinae (*Panchlora*) of the Blaberidae. The hy-

pothesis is presented that stridulating structures in the Oxyhaloinae first evolved, in both sexes, on those parts of the pronotum and tegmina that were rubbed together during struggling movements made when the insects were seized by a predator; originally the sound produced, after stridulating structures evolved, may have had a defensive function. Stridulation by males during courtship has so far been observed only in *Nauphoeta cinerea* (Olivier). Various behavior patterns of males of different blaberids suggest that vibratory and pumping movements, possibly employed to disseminate a pheromone, led to the production of rhythmical sounds in *N. cinerea* which may have sexual meaning to the female.

Relatively little has been done on sound production in cockroaches (Chopard 1938; Frings 1955, 1956; Kevan 1954, 1955; Dumortier 1963). Recently, Dumortier (1965) studied the hissing apparatus in *Gromphadorhina*, and Hartman and Roth (1967a, b) reported on stridulation during courtship behavior in *Nauphoeta cinerea* (Olivier). In this paper we report the results of a study of sound produced by several species of ovoviparous cockroaches (Blaberidae).

MATERIALS AND METHODS

The insects were reared on Purina laboratory chow at 25°–27°C and 45%–55% RH. The methods of recording and determining sound intensity are given in Hartman and Roth (1967a, b). When recording, no effort was made to control the temperature, which ranged from 25° to 29°C. Whole mounts of pronota and tegmina were prepared to study the stridulating structures. Darkly pigmented specimens were first treated with 10% KOH, dehydrated, cleared, and mounted in Permount. The number of striae indicated in the descriptions refers to 1 side of the insect only, unless otherwise stated.

RESULTS

Many cockroaches produce sounds as part of their normal behavior. In general, sounds are made by one or more of the following means: (1) rubbing the abdomen against the wings, (2) tapping the substrate, (3) striking the wings against the abdomen,

(4) expelling air through the spiracles, or (5) scraping the pronotum over the costal veins (stridulation). Each of these sound-production methods will be discussed separately.

I. Sounds not Associated with Specialized Structures

A. *Rubbing the Abdomen Against the Wings.*—Main (1932) noted that a species of *Blaberus* would make "a distinct short hissing sound" when its tegmina were stroked. Main stated that the sound apparently was produced when the abdominal segments were simultaneously contracted toward the thorax. Main was correct in his description of the abdominal movement when *Blaberus* produces sound. We have observed that several species of blaberid cockroaches produce a sound, when restrained, by extending the abdomen posteriorly and then rubbing it anteriorly against the wings. These species are *Blaberus giganteus* (L.), *B. cranifer* Burmeister, *B. discoidalis* Serville, and *Archimandrita tessellata* Rehn. None have a pronotal-tegmina stridulating apparatus and all belong to the Blaberinae (Table 1). Contrary to Chopard (1938, p. 286), *Blaberus* evidently does not have a pronotal-tegmina stridulating apparatus.

The rhythmic disturbance sound made by *Archimandrita* is shown in Fig. 1. This method of sound production is not characteristic of all members of the Blaberinae, since *Eublaberus posticus* (Erichson), *E. distanti* (Kirby), and *Byrsotria fumigata* (Guérin) (males), when restrained, did not rub the abdomen against the wings to produce the sound. Other members of the Blaberidae which apparently do not produce sound in this manner are *Nauphoeta cinerea*, *Leucophaea maderae* (F.), *Diploptera punctata* (Esch-

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scholtz), *Capucina patula* (Walker), *Phortioeca phoraspoides* (Walker), *Pycnoscelus surinamensis* (L.), and *P. indicus* (F.) (formerly considered the bisexual form of *P. surinamensis*; see Roth 1967).

When courting an unreceptive female, *Blaberus craniifer* performs trembling or quivering movements for brief periods after contact. These movements occur in short bursts lasting 1 or 2 sec, with a somewhat shorter rest period between successive bursts. The tegmina are held slightly off the abdomen, while the wings and/or abdomen tremble vigorously. During bursts of trembling, a soft, audible "buzzing"

Table 1.—Species of Blattaria^a which lack stridulatory structures on the pronotum and tegmina.^b

BLATTOIDEA	
BLATTIDAE	
Blattinae.— <i>Blatta orientalis</i> L.; <i>Deropeltis erythrocephala</i> (F.) (♂); <i>Periplaneta americana</i> (L.); <i>P. australasiae</i> (F.); <i>P. brunnea</i> Burmeister; <i>P. fuliginosa</i> (Serville); <i>P. japonica</i> Karny (♂).	
Polyzosteriinae.— <i>Eurycotis decipiens</i> (Kirby); <i>E. floridana</i> (Walker); <i>Methana convexa</i> (Walker); <i>Pelmato-silpha coriacea</i> Rehn; <i>Tenmelytra truncata</i> (Brunner)	
BLABEROIDEA	
POLYPHAGIDAE	
<i>Arenivaga</i> (<i>Arenivaga</i>) sp.; <i>Arenivaga</i> (<i>Psammoblatta</i>) <i>africana</i> L.; <i>A. (P.) cerverae</i> (Bolivar); <i>comp-sodes schwarzi</i> (Caudell); <i>Polyphaga aegyptiaca</i> (L.); <i>Therea petiveriana</i> (L.)	
BLATTELLIDAE	
<i>Aneurita viridis</i> (Hebard) (♀); <i>Arawakina frontalis</i> Hebard (♂); <i>Balta patula</i> (Walker) (♀); <i>B. similis</i> (Saussure) (♀); <i>Burchellia circumcincta</i> (Reiche and Fairmaire) (♂); <i>Ceratinoptera picta</i> Brunner (♀); <i>Euandrobatta propera</i> Rehn (♀); <i>Eumyctibora crassicornis</i> (Burmeister) (♂); <i>Marettina marquesana</i> Hebard (♂); <i>M. uahuka</i> Hebard (♂); <i>Megamareta phanero-pyga</i> (Chopard) (♀); <i>Moluchia castanea</i> (Blanchard) (♀); <i>Nahublattella nahua</i> (Saussure) (♀); <i>Paratem-nopteryx australis</i> Saussure (♀); <i>Pseudothyrsocera rec-tangularivittata</i> (Brunner) (♂); <i>Symplocodes ridleyi</i> (Shelford) (♂); <i>Xosablatta natalensis</i> (Rehn) (♀)	
Anaplectinae.— <i>Anaplecta</i> sp.	
Plectopterinae.— <i>Amazonina</i> sp. nov.; <i>Cariblatta lutea</i> (Saussure and Zehntner); <i>C. minima</i> Hebard; <i>C. sp. nov.</i> ; <i>Chorisonera apolinari</i> Hebard (♀); <i>Dendrobatta sobrina</i> Rehn; <i>Euphyllodromia angustata</i> (Latreille) (♂); <i>Euthlastobatta compsa</i> Hebard (♀); <i>Latiblattella</i> sp. nov. (♀); <i>Lophoblatta arawaka</i> Hebard (♀); <i>L. sp. nov.</i> ; <i>Neoblattella dryas</i> Rehn and Hebard (♀); <i>Onychos-tylus notulatus</i> (Stål); <i>Supella longipalpa</i> (F.) (formerly <i>S. supellecillum</i> (Serville))	
Blattellinae.— <i>Blattella germanica</i> (L.); <i>B. humbertiana</i> (Saussure); <i>B. unicolor</i> (Brunner); <i>Ischnoptera dero-peltiformis</i> (Brunner); <i>I. panamae</i> Hebard; <i>I. rufa rufa</i> (Degeer); <i>Parcoblatta bolliana</i> (Saussure and Zehntner) (♂); <i>P. pensylvanica</i> (Degeer); <i>P. uhleriana</i> (Saus-sure) (♂); <i>P. virginica</i> Brunner (♂); <i>Pseudomops in-tercepta</i> (Burmeister) (♂); <i>P. septentrionalis</i> Hebard (♂); <i>Shawella coulomiana</i> (Saussure); <i>Symploce hospes</i> (Perkins); <i>Xestoblatta immaculata</i> Hebard	
Ectobiinae.— <i>Ectobius lapponicus</i> (L.) (♀); <i>E. pallidus</i> (Olivier) (♀); <i>Phyllodromica</i> (<i>Luridiblatta</i>) <i>trivittata</i> (Serville) (♂)	
Nyctiborinae.— <i>Megaloblatta blaberoidea</i> (Walker) (♂); <i>M. regina</i> (Saussure); <i>Nyctibora azteca</i> Saussure and Zehntner (♂); <i>N. laevigata</i> (Beauvois) (♂); <i>N. tetrasticta</i> Hebard (♂); <i>N. tomentosa</i> Serville (♂)	

Table 1.—Species of Blattaria^a which lack stridulatory structure on the pronotum and tegmina.^b (Continued.)

BLABERIDAE	
Zetoborinae.— <i>Phortioeca phoraspoides</i> (Walker)	
Blaberinae.— <i>Archimandrita tessellata</i> Rehn; <i>Blaberus craniifer</i> Burmeister; <i>B. discoidalis</i> Serville; <i>B. giganteus</i> (L.); <i>Byrsotria fumigata</i> (Guérin); <i>Eublabeus distantis</i> (Kirby); <i>E. posticus</i> (Erichson)	
Panesthiinae.— <i>Panesthia australis</i> Brunner (♂); <i>P. laevicollis</i> Saussure (♀)	
Pycnoscelinae.— <i>Pycnoscelus indicus</i> (F.)	
Diplopterinae.— <i>Diploptera punctata</i> (Eschscholtz)	
Panchlorinae.— <i>Capucina patula</i> (Walker)	
Oxyhaloinae.— <i>Heminauphoeta hova</i> Saussure and Zehntner (♀); <i>Oxyhaloa deusta</i> (Thunberg) (♀)	
Epilamprinae.— <i>Ataxigamia tatei</i> Tepper (♂); <i>Audreia jamaicana</i> Rehn and Hebard (♀); <i>Laxta graminicollis</i> (Saussure) (♂); <i>Litopeltis bispinosa</i> (Saussure) (♂)	
Perisphaeriinae.— <i>Gyna capucina</i> Gerstaecker (♂); <i>G. sculpturata</i> Shelford (♂)	

^a Classification principally according to McKittrick (1964, and personal communication) and Princis (1960).

^b Females of the Polyphagidae listed (except *T. petiveriana*) lack tegmina and therefore only males were examined. Otherwise, where no sex symbol appears, both sexes were examined and found to lack stridulatory structures.

sound is produced (Barth 1961). It is possible that this sound is produced by rubbing the abdomen against wings.

During courtship, the male of *Eublabeus posticus* pulses the abdomen back and forth and lifts the wings off the abdomen. Both the tegmina and abdomen vibrate and the male may butt the female with his head. The abdomen is curved downward slightly (wings horizontal) and is not much extended during the pumping motions; the tegmina vibrate at about the same frequency. A not very rhythmic rustling sound (Fig. 2) is produced. We are not certain how this sound is produced.

B. Tapping the Substrate.—Some species of blaberids produce sounds by striking the abdomen against the substrate during courtship. The sound produced by males of *Leucophaea maderae* during courtship is probably the oldest and best documented example of a cockroach sound made by tapping (see Dumortier 1965). Details of this behavior are given by Barth (1961) and Roth and Barth (1967). Often during antennal fencing with the female, the male of *L. maderae* performs repeated high-frequency, small-amplitude, vertical jerks of the body; the abdomen moves down as the head and prothorax move upward. An audible tapping sound may be associated with this movement. Vertical vibration occurs in bursts lasting about 5 sec, though this apparently may vary with the receptivity of the female. The bursts are interspersed with brief rest periods, each lasting a few seconds. The wings may be raised up to 30° off the abdomen during later stages of vertical vibration. If the female is receptive, the male's vibrating movement is usually omitted, and he raises his wings to an angle of 60°–80° above the horizontal. Unreceptive females may be induced to mount the male after a prolonged courtship involving vertical vibration on the part of the male. However, mating does not occur even though the female may feed

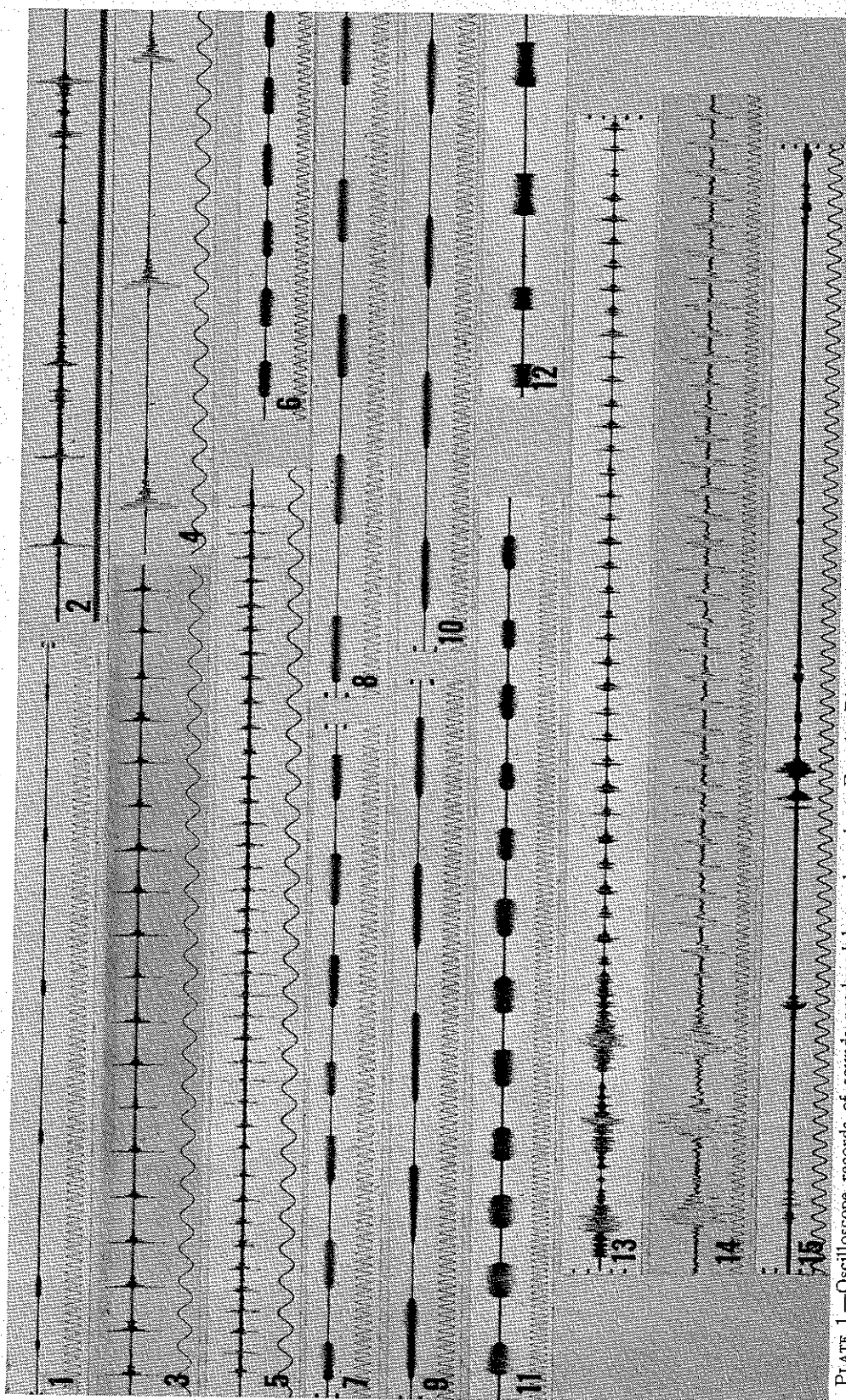


PLATE 1.—Oscilloscope records of sounds produced by cockroaches. FIG. 1.—Rhythmic disturbance sounds made by a *Archimandrita tessellata* held 2 cm from the microphone. FIG. 2.—Arhythmic rustling sound made by a courting *Eublaberus posticus*. FIG. 3.—Sound produced by a *Leucophaea maderae* tapping upon the substrate, which, in this case, was a ♀ upon which the ♂ was standing. FIG. 4.—Same record as in FIG. 3, filmed at higher speed. FIG. 5.—Courting sounds produced by a *Diploptera punctata* by striking the wings against the abdomen. FIG. 6-12.—Disturbance hisses made by species of *Gromphadorhina*. 6, *G. javanica* ♂. 7-8, *G. portentosa* ♂ and ♀, respectively, held about 15 cm from microphone. 9-10, *G. brunneri* ♂ and ♀, respectively, held about 15 cm from microphone. 11-12, *G. chopardi* ♂ and ♀, respectively. FIG. 13-15.—*Nauphoeta cinerea*. 13, phrase produced by stridulation during courtship by a ♂ at 1 cm from microphone. 14, substrate recording of a phrase produced by a ♂ during courtship stridulation. 15, disturbance sound produced by the ♂ while being handled 3-5 cm from microphone. Sound-level reference marks are 65 db in FIG. 1 and 15; 70 db in FIG. 7-10; and 60 and 65 db in FIG. 13. Reference signals are 20 Hz for FIG. 1 and 5-14; 100 Hz for FIG. 2; 10 Hz for FIG. 3 and 15; and 50 Hz for FIG. 4.

briefly on the tergal gland secretion (Barth 1961, Roth and Barth 1967). The tapping sound is very rhythmical (Fig. 3, 4) and is made when the abdomen strikes the substrate. However, the pumping rhythm is still audible even though the abdomen fails to contact the substrate. In the example illustrated, the male was standing atop the female and used her as the substrate. The tap rate in this case was 7/sec. It is of interest that *isolated* males may perform vibratory movements and tap the substrate.

The males of *E. posticus* also may make a tapping sound during courtship, apparently when the end of the abdomen strikes the substrate. However, the vibrating motion is not as marked as in *Leucophaea*. Barth (1964) observed males of *Byrsotria fumigata* tapping during courtship.

C. Striking the Wings Against the Abdomen.—During courtship, the male of *Diploptera punctata* raises its tegmina and may flutter its wings (Roth and Willis 1955, Stay and Roth 1958). According to Barth (1961), the tegmina are pumped up and down "while the wings are fluttered, producing a barely audible whirring sound. This display may last several seconds and may be repeated a number of times, particularly if the female is relatively unresponsive." We have observed this behavior under a microscope using stroboscopic lighting and we have also recorded the sound, which is quite rhythmic (Fig. 5). The tegmina are raised off the abdomen and held slightly apart. The wings are not moved in a scissorlike motion; rather, they remain folded and move up and down, producing the sound principally by striking the abdomen. The fluttering rate depicted (Fig. 5) is about 29/sec. Courting males whose tegmina have been removed can still produce the sound.

II. Sounds Produced by Specialized Morphological Structures

A. Spiracular Sound-Producing Organs.—The cockroaches known to produce sound by expelling air through the second abdominal spiracles are wingless forms of the genus *Gromphadorhina*. They are endemic in Madagascar. One species, *G. javanica* Hanitsch, was erroneously reported to have come from Java (Hanitsch 1930), but it also is found in Madagascar (Princis 1965). Because of the intense, characteristic hissing sound produced by these insects, they are called "blowers" by the Europeans of Madagascar, "Sanda" in Veza and Mahafaly dialects (Wintrebert in Dumortier 1965), and "Kofokofoka" in the high-plateau dialect (Chopard 1950). The morphology of the tracheal sound-producing device has recently been described and is present in *G. coquereliana* Saussure, *G. portentosa* (Schaum), and *G. brunneri* Butler (Dumortier 1965). We have found that *G. javanica* and *G. chopardi* Lefevre also produce a hissing sound when handled.

In *G. brunneri* (Dumortier 1965) and *G. portentosa* (Barth 1961), males hiss in defense of territory, and the latter hisses when it courts the female (Barth 1961). The female of *G. brunneri* hisses only when disturbed (Dumortier 1965), and *G. portentosa* does

so particularly if disturbed when young are present (Roth and Willis 1960).

Fig. 6-12 are records of hisses produced by 4 species of *Gromphadorhina* when disturbed. These insects were held about 15 cm from the microphone, and were encouraged to hiss by the operator's pulling a leg with a pair of forceps. The *G. javanica* male in Fig. 6 hissed at the rate of 2.5/sec, with a hiss duration of 240 msec. The females of *G. javanica* do not hiss readily.

Both sexes of *G. portentosa* produce disturbance sounds readily. Their sounds, shown in Fig. 7 and 8, are produced at a rate of about 2/sec by the male and 2.5/sec by the female. The hiss durations are 320 msec and 400 msec, respectively, and the intensity in both cases exceeds 65 db.

Disturbance sounds by *G. brunneri* are shown in Fig. 9 and 10. The male hisses at the rate of 1.3/sec, the hiss having a 520-msec duration. The female produces hisses at the rate of 1/sec, and the hisses have a 480-msec duration. The intensity of these sounds also exceeds 65 db.

The *G. chopardi* male disturbance sounds are delivered at the rate of 2.5/sec, with each hiss having a 220-msec duration. However, the female does not hiss readily, and when she does, the hisses are not so uniformly spaced as in the male (cf. Fig. 11 and 12).

B. Sound Production by Distinctive Stridulating Structures.—Stridulation is known to occur in both sexes of *L. maderae*, *N. cinerea* and *Henschoudekenia epilamproides* (Shelford). The stridulating apparatuses in *Leucophaea* and *Nauphoeta* are very similar, and consist of parallel striae on the ventral lateroposterior margins of the pronotum and on the dorso-proximal regions of the costal veins of the tegmina.

Vosseler (1907), who first described the stridulating apparatus of *L. maderae* (Fig. 21-24), claimed that *Leucophaea* stridulated only when captured or "frightened." He concluded (after studying dead specimens) that the sound is produced when the insect rubs the pronotum sideways against the proximal region of the costal veins. In the male, there are about 50 striae on the pronotum (2 specimens) spaced about 4 μ apart, and between 700 and 900 striae on the costal vein (3 specimens). Nothing is known about stridulation in this species other than that they stridulate when disturbed. We have not heard them stridulate during courtship.

Hartman and Roth (1967a, b) reported on courtship stridulation by *N. cinerea*. The male possesses about 40 striae on the pronotum (Fig. 16-18, 20) and about 400 on the costal vein of the tegmen (Fig. 19). The striae on both structures are about 4 μ apart. Both sexes produce disturbance sounds (Fig. 15). The arhythmic disturbance sounds illustrated were made by a male held 3-5 cm from the microphone. These noises were quite loud, exceeding 70 db, and are the result of relatively uncoordinated lateral pivoting of the pronotum across the costal veins. However, the male produces a patterned call (Fig. 13) by coordinated movements when it courts an unreceptive female (Fig. 33, 34). This sound is

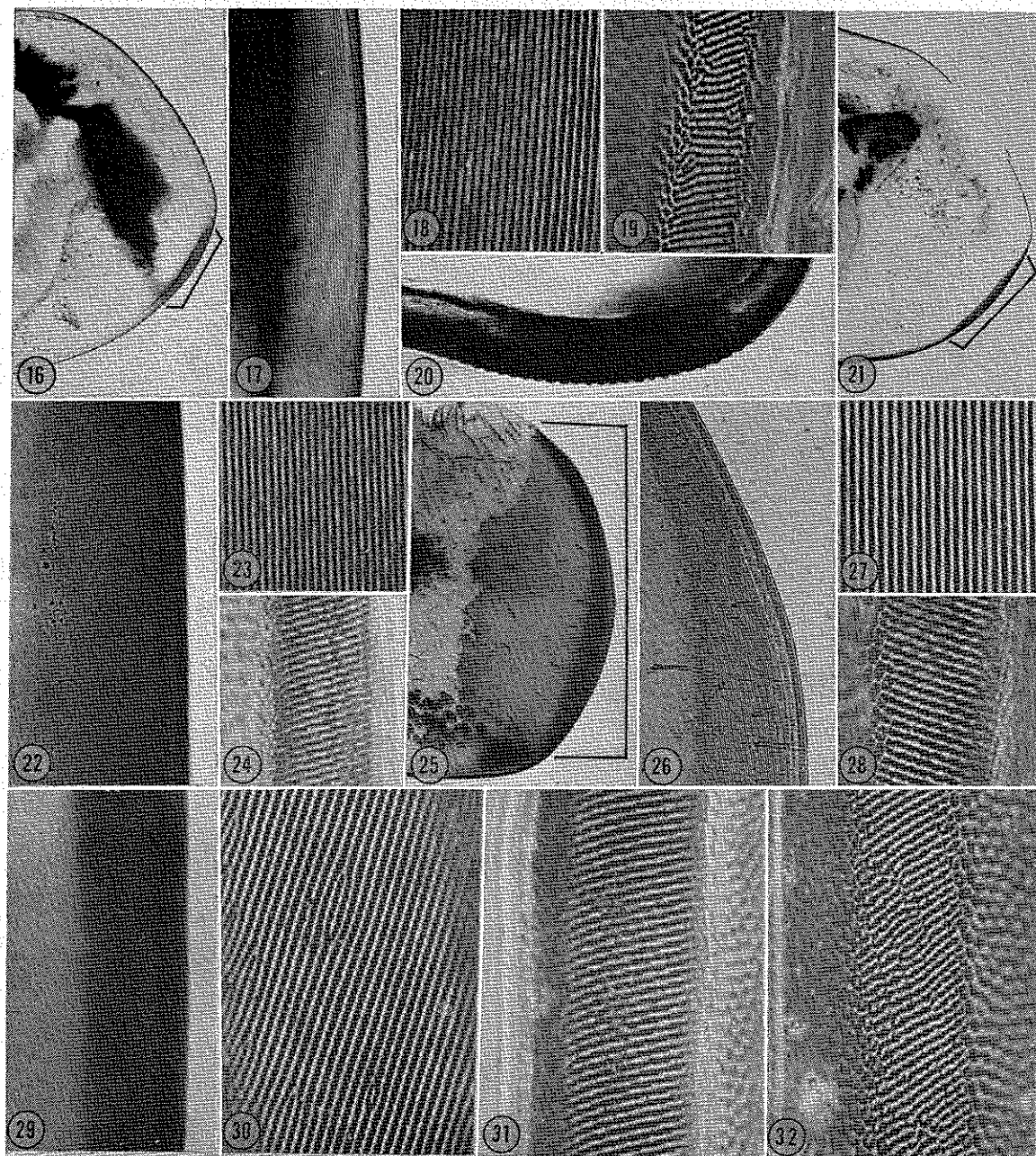


FIG. 16-32.—Stridulating structures on the pronota and tegmina of *Nauphoeta*, *Leucophaea*, *Henschoudekenia* and *Jagrehnia*.

FIG. 16-20.—*Nauphoeta cinerea* ♂, from Natick culture. 16, right side of pronotum; the striae are located in bracketed pigmented area, $\times 8.2$. 17, portion of striae on pronotum, $\times 102$. 18, portion of striae on pronotum, $\times 291$. 19, portion of striae on tegmen, $\times 291$. 20, cross section of the striae on pronotum, $\times 371$.

FIG. 21-24.—*Leucophaea maderae*, from Natick culture. 21, right side of ♀ pronotum; striae are situated in bracketed pigmented area. 22, portion of striae on ♀ pronotum, $\times 102$. 23, portion of striae on ♀ pronotum, $\times 291$. 24, portion of striae on ♂ tegmina, $\times 291$.

FIG. 25-28.—*Henschoudekenia flexivitta* ♀, from Natick culture. 25, portion of right side of pronotum, $\times 15$; striae are found on bracketed pigmented area. This specimen was damaged so that anterior limit of area covered by striae is not shown. 26, portion of striae on pronotum, $\times 60$. 27, portion of striae on pronotum, $\times 291$. 28, portion of striae on tegmen, $\times 291$.

FIG. 29-32.—*Jagrehnia gestroiana* ♀, from Somalia. 29, portion of striae on pronotum, $\times 102$. 30, portion of striae on pronotum, $\times 291$. 31, portion of striae on tegmen, $\times 291$. 32, apical portion of striae on tegmen, near region where striae blend into wing sculpturing, $\times 291$.

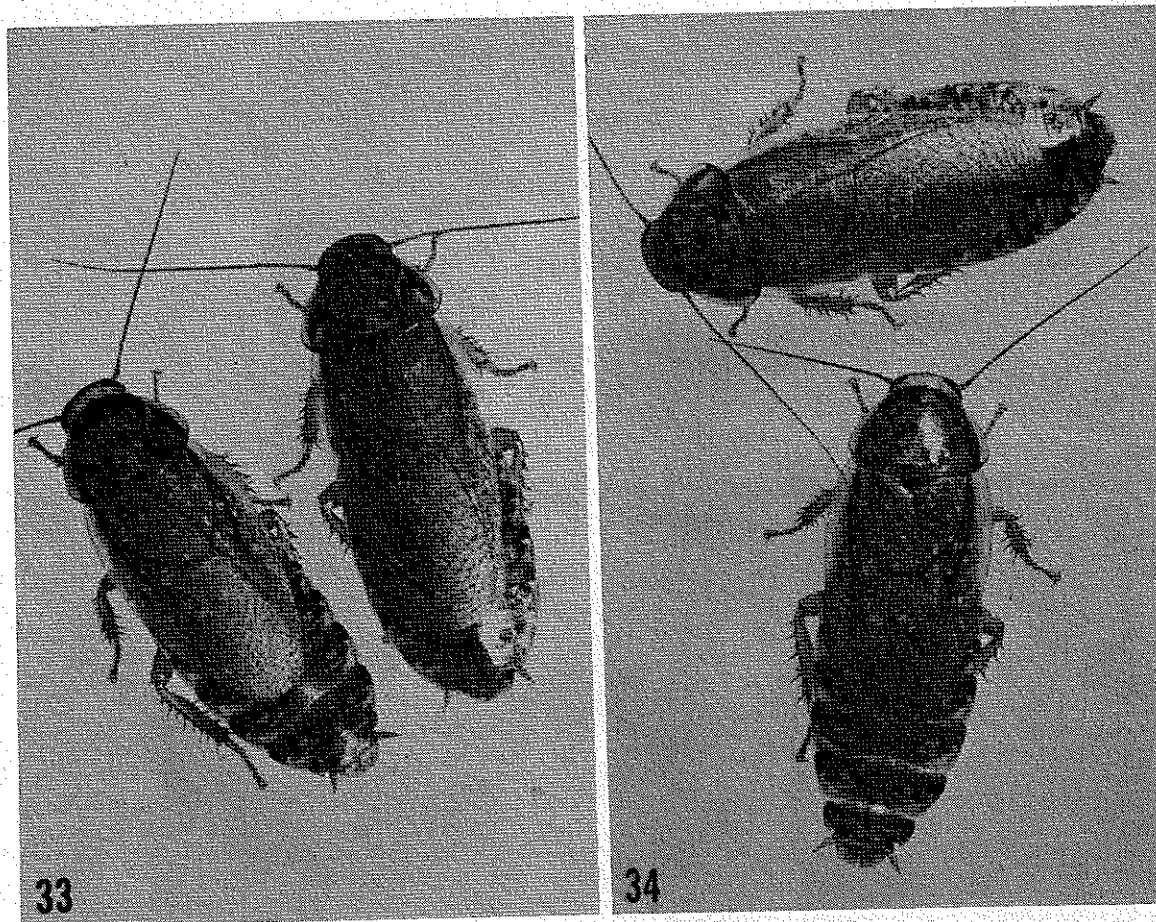


FIG. 33-34.—*Nauphoeta cinerea*. 33, male (left) prior to stridulating. 34, male (below) stridulating.

produced by posterior, anterior, and side-to-side displacement of the pronotum rubbing against the costal veins.

Guthrie (1966) described the sound produced by *H. epilamproides*, a species of cockroach which stridulates when it is disturbed. The stridulatory apparatus is similar to that found in *Leucophaea*, *Nauphoeta*, and *Henschoudetenia flexivitta* (Walker) (see following). According to Guthrie, the striae are about 5μ apart. The sound intensity rises to about 70 db and there is a carrier wave form of about 5 kc/s, amplitude-modulated to form pulses at 1-2 kc/s. The pulses form chirps of 100 msec or longer, and are simple or complex in structure. He noted that the recorded cockroach sound caused wild bank voles to run away.

Both sexes of *Panchlora nivea* (L.) possess a stridulating apparatus. The striae on the pronotum are often difficult to see, and many do not run the full length of the posterior lateropronotal margins (Fig. 38). One male had 14 striae on one side and 15 on the other, the striations being about 3μ apart. The rodlike structures (Fig. 35, 36) on the tegmina are arranged just below the costal vein. One female of *P. nivea* had 50 striae, and a male had 35, the spacing in both individuals being about 19μ - 21μ .

We have observed *P. nivea* males stand and vibrate their bodies near a female while courting. However, we have been unable to hear or record any sound (Hartman and Roth 1967b) even though the movements are very similar to those of a stridulating male of *N. cinerea*. *Panchlora irrorata* Hebard performs similar vibratory motions when courting the female (Willis 1966) as a preliminary to successful mating. Both sexes of *P. irrorata* possess stridulating structures (Fig. 37, 39). A male had 26 striae on each tegmen and a female had about 30. Very fine striae are also present on the pronotum (Fig. 39). The striae on the tegmina are not so well differentiated as in *P. nivea* (cf. Fig. 35, 36).

A survey was made of museum specimens of Blattodea and other Blaberoidea for the presence of stridulating structures on the pronotum and tegmina. They were absent in all Blattidae, Polyphagidae, and Blattellidae examined, as well as 21 Blaberidae (Table 1), but they were present in 3 genera belonging to the Oxyhaloinae.

The striae on the pronotum and tegmina of the *Jagrehnia gestroiana* (Saussure) (Fig. 29-32) female are very similar to those found in *Nauphoeta*, *Henschoudetenia*, and *Leucophaea*. The striae on the pronotum of *Jagrehnia* differ from those of the other

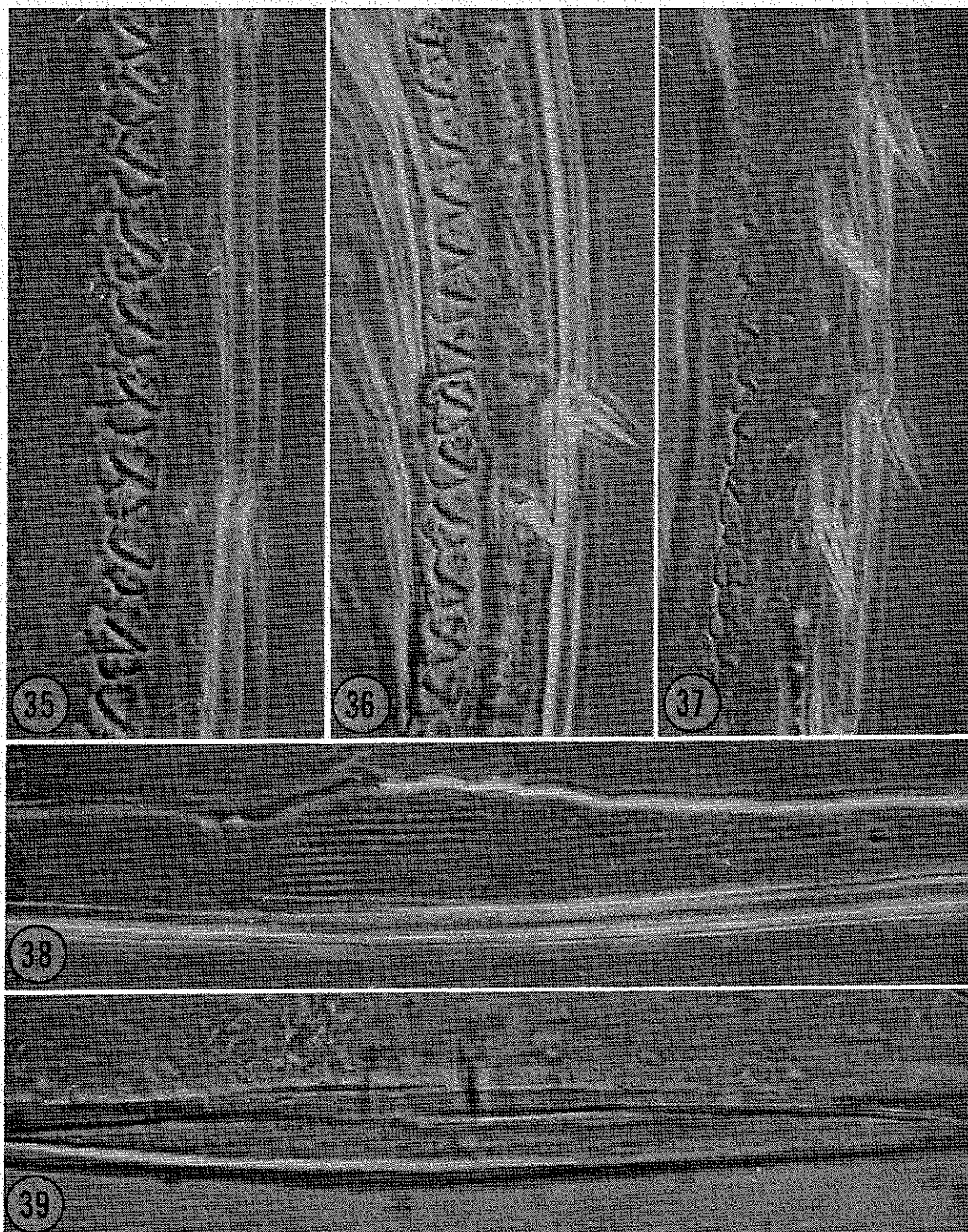


FIG. 35-39.—Stridulatory structures in *Panchlora*, $\times 485$. 35, *P. nivea* ♀ from Natick culture, part of file on right tegmen. 36, *P. nivea* ♂, part of file on right tegmen. 37, *P. irrorata* ♂, adventive from Illinois, part of file on right tegmen. 38, *P. nivea* ♂, file on 1 side of pronotum. 39, *P. irrorata* ♀, file on 1 side of pronotum.

genera in that they are shorter, run obliquely (cf. Fig. 29 with Fig. 17, 22, and 26), and are much more numerous.

The pronotal-tegmina structures (Fig. 25-28) of the female of *H. flexivitta* are typical of those previously described, except that the striae cover a great part of the lateral margins of the pronotum; these striae extend over the anterior as well as posterior-lateral pronotal margins (Fig. 25). The female that was examined had about 65 striae on the pronotum, spaced approximately 4.7μ apart, and about 500 striae on the tegmen.

The stridulating apparatus on the tegmina of the *Oxyhaloa* species examined (Fig. 40-51) differs markedly from those previously described. The striae occur in distinct, separated patches of tubercles or crests along side the proximal region of the costal veins.

The single male specimen of *Oxyhaloa buprestoides* (Saussure) had 4 distinct patches on the left side (Fig. 40) and 5 on the right side (Fig. 41). The size of each group of striae is variable. Two females of this species were examined. One had 2 groups of striae on the left side (Fig. 42, 44), the second group smaller than the first. The same number of groups of striae are found on the right side (Fig. 43, 45) but the posterior group is relatively poorly developed. Another female also had 2 groups of striae on each tegmen (Fig. 46, 47).

Another *Oxyhaloa* species (probably *ferreti* (Reiche and Fairmaire)) had stridulating structures. On the male there are 2 well-developed groups of tubercles on the left tegmen (Fig. 48) and 3 groups on the right (Fig. 49). The right tegmen of the female has 2 groups of tubercles (Fig. 52) and, as in *O. buprestoides*, the second group is smaller than the first. There are no distinctive tubercles on the left tegmen of this female, but several peculiar aberrant patches (Fig. 50, 51) are present.

A female of *Oxyhaloa deusta* (Thunberg) lacked stridulating structures on the tegmina.

In both species of *Oxyhaloa* that had tegmina striae, the pronotum apparently lacks a stridulating structure, but it is conceivable that the edge of the pronotum may be used to rub against the tegmen. In *N. cinerea* the male can produce its courting sound, although the pronotal striae are cut off; in this experimental situation, the edge of the cut surface of the pronotum rubs against the tegmen (Hartman and Roth 1967b). Unfortunately, no observations of sound production have been made on living *Oxyhaloa*.

Of the large number of species and genera examined that lacked stridulating structures (Table 1), only 2 species had modifications of the tegmina (but not on the pronota) which were suggestive of striae. In a male of *Catara rugosicollis* (Brunner) (Blattidae) the tegmina sculpturing on the basal region of the costal vein was arranged to form faint parallel lines (reminiscent of *Nauphoeta*, etc.). These were difficult to see because the surface appeared smooth and the lines may simply be lightly pigmented areas (Fig. 53). In both sexes of *Gislenia australica* (Brun-

ner) (Blattellidae: Blattellinae) the surface of the tegmina alongside the basal region of the costa is wrinkled and some areas show distinct, ridgelike elevations reminiscent of, but not so uniform as the file in *Panchlora* spp. These modifications are more distinct in the female than in the male, but in both sexes the size and number of "files" vary from 1 specimen to the next (cf. Fig. 54, 55) and also vary on the right and left tegmen of the same specimen (Fig. 54). The tegmina modification of *Gislenia* may represent a very early stage in the evolution of striae on the tegmina of some Blaberidae.

III. Sound Production in Other Blattaria

With the exception of *Catara* and *Gislenia*, all the cockroaches discussed previously in this paper belong to the highly evolved Blaberidae and are ovoviviparous or viviparous (*Diploptera*). Almost nothing is known of sound production in oviparous cockroaches. Baier (1930) suspended a microphone among a group of *Blattella germanica* (L.) and could not detect any sound production.

Kleine (1918) was awakened by a sound like that produced by a locust, but not so pure. The only insect in the room was *Blatta orientalis* L. (Blattidae: Blattinae). On another occasion, he and an entomologist visiting him heard the same sound, and again the only insect in the room was the *B. orientalis*.

Rudow (1870, p. 322) claimed that *Ectobius lapponicus* (L.) (Blattellidae: Ectobiinae), when disturbed, made a short, abrupt, clicking sound before taking to flight. He assumed that the same sound could be made by rubbing the tegmina together. Karny (in Shelford 1909) suggested that the ulnar rami of the wings in *Gyna caffrorum* (Stål) (Blaberidae: Perisphaeriinae) can produce a rattling noise when the insect flies. Karny described this species as *G. stridulans*.

According to Skaife (1954) when the wingless female of the African species *Aptera fusca* (Thunberg) (Blaberidae) is handled, it makes a squeaking sound by rubbing the roughened edge of 1 segment of the abdomen against the surface of the next segment.

Karny (1924) described a stridulating apparatus on the hind wing rudiment and first abdominal tergite of females of *Archiblatta hoeveni* Vollenhoven (Blattidae). Since the males lacked this structure and small colonies consist of "mothers" and young, Karny suggested that the sound is used to keep the "brood" together. However, Karny produced the sound in dead females only by flexing the anterior and hind ends of the abdomen ventrally, and his conclusion is purely speculative.

We have heard a female of the wingless *Euzosteria nobilis* (Brunner) (Blattidae: Polyzosteriinae) produce a faint, squeaking sound when held. Slides were made of the entire abdomen and thorax, but no stridulating structures were found. The site of sound production in this species is unknown.

DISCUSSION

Two distinct mechanisms for sound production—

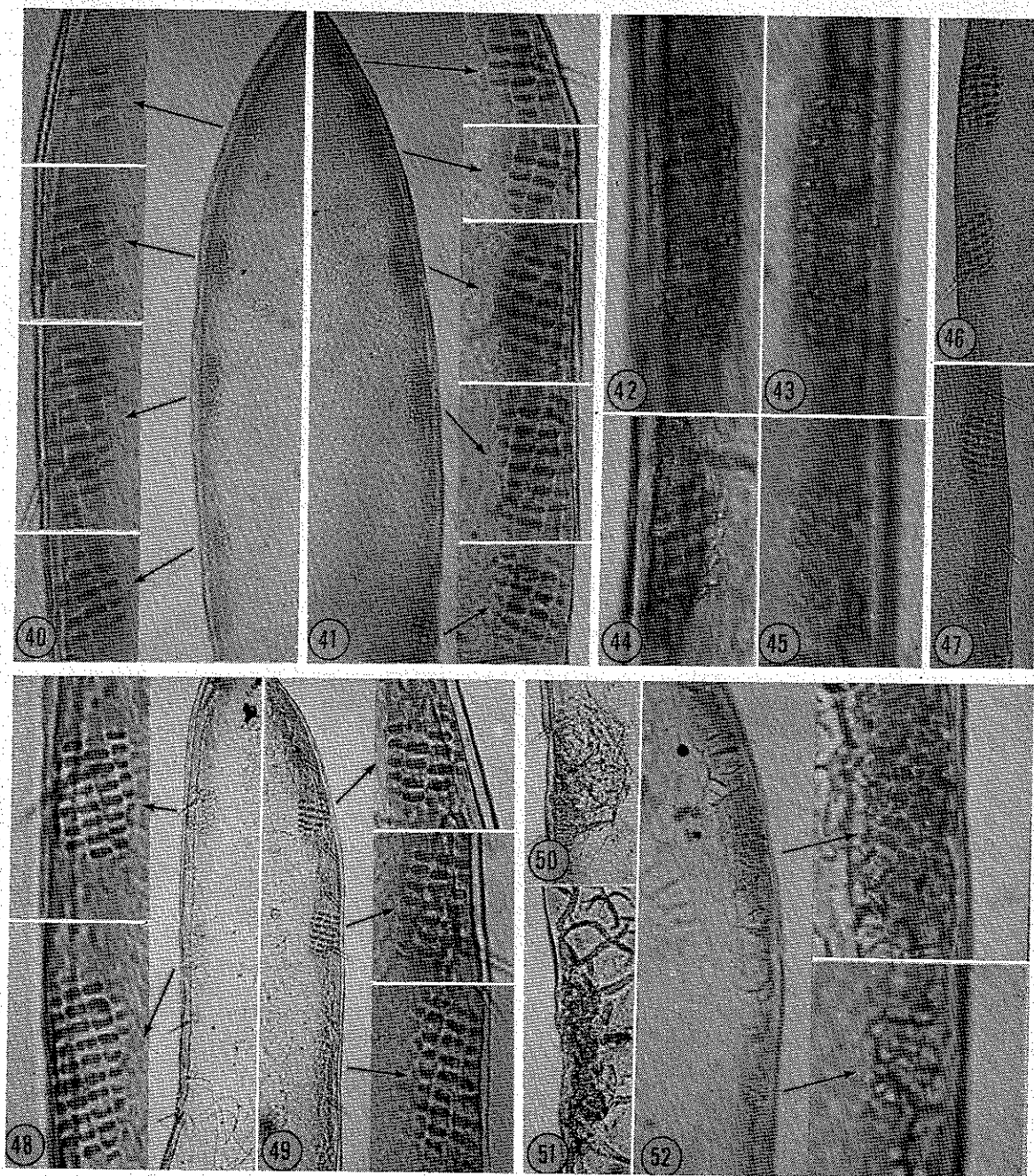


FIG. 40-47.—Stridulatory structures on the tegmina of *Oxyhaloa buprestoides*. 40, ♂ from Ruanda: Nguda (Cheff.) Terr. Nyanza; part of left tegmen, showing separated patches of striae, $\times 122$ (arrows point to enlarged views, $\times 317$, of respective groups of striae. 41, same as Fig. 40; right tegmen. 42-43, ♀ from Victoria, Njansa; patch 1 on left (42) and right (43) tegmina, $\times 317$. 44-45, same as 42-43; patch 2 on left (44) and right (45) tegmina, $\times 317$. 46-47, ♀ from Ruanda, Terr. Shangugu, Dendezi; patches on left (46) and right (47) tegmina, $\times 122$.

FIG. 48-52.—Stridulatory structures on tegmina of *Oxyhaloa* sp. (probably *O. ferreti*). 48, ♂ from Ethiopia; part of left tegmen, showing separated patches of striae, $\times 123$ (arrows point to enlarged views, $\times 317$, of respective patches). 49, same as Fig. 48, right tegmen. 50-51, ♀ from Ethiopia; 2 of several aberrant patches on left tegmen. 52, same as Fig. 50-51; right tegmen, showing 2 patches, $\times 123$ (arrows point to enlarged views, $\times 317$, of striae).

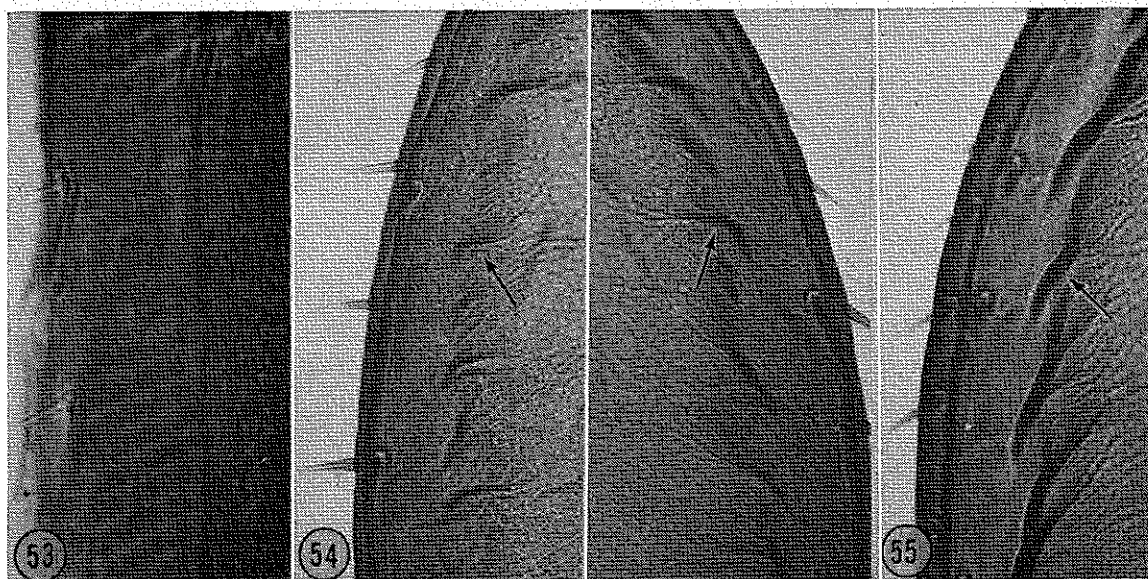


FIG. 53-55.—Portions of the tegmina of *Catara* and *Gislénia*. 53, *Catara rugosicollis* ♂; small area of proximal part of left tegmen, showing fine, light lines that appear to be striae, $\times 354$. 54-55, *Gislénia australica*, 54, proximal regions of right and left tegmina of ♀, showing some of the ridges (arrows) below the costal veins, $\times 137$. 55, proximal region of left tegmen of ♂, showing several thick, raised ridges, $\times 137$.

stridulation and expulsion of air through abdominal spiracles—have evolved in the Panchloroid complex of the Blattaria. Within this complex, these mechanisms are represented only in the Oxyhaloinae and Panchlorinae. *Nauphoeta*, *Leucophaea*, *Oxyhaloa*, and *Gromphadorhina* are all members of the Oxyhaloinae (McKittrick 1964). *Henschoutedenia* and *Jagrehnia* were originally split off from the genus *Nauphoeta* (Princis 1954), and for this reason we place the former 2 genera in the Oxyhaloinae also.

The striae forming the stridulating structures appear to have evolved as thickenings or modifications of the reticulate sculpturing of the surface on which they are found. This condition is especially noticeable in areas where the striations gradually merge into the sculpturing of the surfaces of the tegmina (Fig. 32). Although the tegminal striae of *Oxyhaloa* (Oxyhaloinae) and *Panchlora* (Panchlorinae) look quite different from those found in other genera of Oxyhaloinae (i.e., *Nauphoeta*, *Leucophaea*, and *Henschoutedenia*), they also appear to have evolved as modifications of the tegminal surface sculpturing.

Locomotor, feeding, and cleaning movements have been suggested as having led to frictional stridulatory mechanisms in insects (see review by Haskell, 1964). We suggest that in certain species of blaberid cockroaches, struggling movements made by the insect when it was seized by a predator led to the formation of a specialized sound-producing apparatus on the pronotum and tegmina. In the Hemiptera "the chance production of sounds by the movement of one part of the body over another could have developed on the one hand into a deterrent to predators, and on the other into a means of ensuring the meeting of the sexes." (Leston and Pringle 1963.)

When highly developed stridulating structures are present in adult cockroaches, they occur in both sexes. Any hypothesis concerning the evolution of stridulation in the Blattaria must account for the presence of equally developed stridulating structures in both male and female. Although it has been suggested that the females of some Blaberidae employ sound to maintain the mother-young group (Dumortier 1965), there is no experimental evidence for this hypothesis (Hartman and Roth 1967b). It is probable that these devices for sound production originally served a non-sexual function—possibly they played a role in defense against predators. Only a relatively small part of the stridulating area is used by *Leucophaea* when "protesting" (Vosseler 1907) and *Nauphoeta* probably uses even less when stridulating during courtship. When *Nauphoeta* is physically restrained, its struggles and pronotal movements are vigorous and more stridulating surface is used in producing sound than during courtship; this probably accounts for the greater intensity of the disturbance sound, as compared with that made during courtship. The area bearing pronotal stria in *Henschoutedenia* (Fig. 25) is considerably greater than that found in the other Oxyhaloinae examined; this may represent a more primitive condition and suggests that in *Leucophaea* and *Nauphoeta* there has been a reduction in the stridulating surface area on the pronotum.

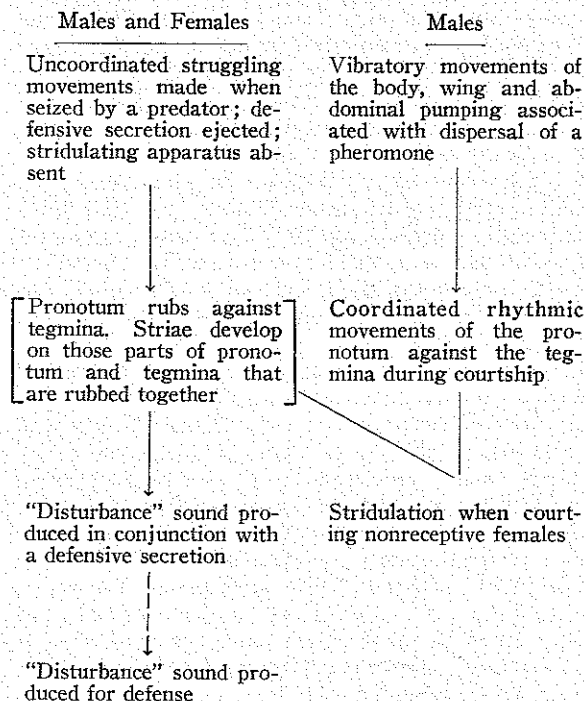
Gromphadorhina nymphs and adults produce sound, and it is likely that the tracheal sound apparatus also evolved as a defensive mechanism. The expulsion of air through the second abdominal spiracles could have been associated with ejection of defensive compounds. Barth (1961) claimed that an odor was associated with sound production in *G. portentosa* but Dumortier (1965) could not confirm this hypothesis.

in *G. brunneri*. In *D. punctata*, quinones used in defense are ejected from the second abdominal spiracles (Roth and Stay 1958, Eisner 1958). When *Diploptera* is anesthetized, it ejects its quinones and we have heard a weak squeaking sound produced (apparently originating from the second abdominal spiracles) when this occurs. When seized, *Leucophaea* gives off an offensive odor which originates from glands emptying into the second abdominal spiracle (Roth and Stay 1958); this cockroach may also stridulate at this time. Pumphrey (1955, in Dumortier 1963) suggested that the combination of sound production with the simultaneous release of an irritating chemical may cause the predator to associate a sound with an unpleasant experience; this could result in sound alone eventually becoming an effective predator deterrent. Dumortier (1965) questions the value of hissing by *Gromphadorhina* as a means of protection from natural predators. Although a dog retreated from a hissing *G. portentosa* (Roth, in Dumortier 1965) Dumortier dismisses this observation because the dog does not normally feed on this cockroach. He observed that a kinkajou and some jays ate *Gromphadorhina* in spite of hissing. However, neither the kinkajou (South American) nor jays, though both are carnivorous, could be considered natural predators of this cockroach since they do not occur in Madagascar. In this connection, it is known that even chemical defensive mechanisms may be effective against some predators but not others (Roth and Willis 1960). A study of the ecology of *Gromphadorhina* may reveal the presence of predators in its environment which are deterred by the hissing sound made by members of this genus.

How has stridulation evolved as a behavioral mechanism for courtship in the males of *N. cinerea*? Trembling or vibratory movements are characteristic of stridulation in *Nauphoeta*. This type of behavior is not uncommon in species of blaberids that lack stridulatory structures, particularly when courting males are confronted with an unreceptive female. The vibratory movements of males of *Blaberus giganteus* and *B. craniifer* become continuous and vigorous if the female is unreceptive (Barth 1961). Males of *Byrsotria fumigata* pump the abdomen and wings prior to full wing raising during courtship. Should the female be unreceptive, the wing pumping may be continued for several minutes (Barth 1964). Comparison of the behavior patterns made by different species suggests that the various wing and body movements made during courtship could be associated with dissemination of a pheromone used to induce the female to mount the male, and thus maneuver her into the proper position for copulation. The movement of the abdomen against the wings may first serve to transfer male pheromone from the terga to the wings and when the wings are finally raised during courtship or are fluttered, there is a greater dispersion of the pheromone. Males of *Diploptera punctata*, which raise the tegmina and beat the wings against the abdomen, would appear to have the most effective means of disseminating a pheromone.

In *N. cinerea*, the male stridulates during courtship, usually if the female is unreceptive. Stridulation apparently has evolved in *Nauphoeta* males as a means of promoting receptivity in the female. Yet we have been unable to show that male stridulation influences a nonreceptive female's behavior. Perhaps the female responds to the male's stridulation only when it is on the verge of becoming receptive. Skinner (1966) stated that "Useless structures with associated useless functions are as inevitable as superstitious ['ritualistic'] behavior." Perhaps male courtship stridulation by *Nauphoeta* is a useless function now and it may represent a stage of evolution prior to its becoming sexually meaningful to the female.

Our hypothesis of how courtship stridulation has evolved in the male of *N. cinerea* may be summarized as follows:



In *Panchlora nivea* there may be no discernible preliminary courtship by the male if the female is receptive. However, if the female is unreceptive, the male behaves differently and performs vibratory movements (Roth and Willis 1958). Interestingly, the male of *P. irrorata* performs vibratory movements prior to successful mating with a receptive female (Willis 1966). This fact suggests that sounds or vibration of the substrate (see following) may be involved in releasing the female's sexual behavior. In both *P. nivea* and *P. irrorata*, the female does not feed on the male's terga prior to copulation; the male backs into the female to make connection, and there is no male tergal secretion. *Panchlora* probably evolved from a stock in which the males produced a tergal secretion and this genus may represent a group in which the pheromone has been lost, but the

males have retained the vibratory movements which may have sexual meaning to the female.

In *Leucophaea maderae* the female is attracted to the male by odor (Smyth 1963, Roth and Barth 1967), but males may vibrate the body and tap the substrate even when isolated. This type of sound production (as well as stridulation in *Nauphoeta*) could have been the forerunner of acoustic "calling" devices to attract the female.

The fact that *Nauphoeta cinerea*, stridulates during courtship tends to support Alexander's (1956) hypothesis regarding the evolution of stridulation. In discussing the evolution of air-transmitted vibrations in the Ensifera (Tettigoniidae, Gryllidae, Gryllacridae, and Prophalangopsidae), Alexander suggested that substrate-transmitted vibrations produced by stridulation or body-jerking was an intermediate stage between proprioception and perception of air-borne sound. He stated that "some of the structural and functional precursors of tegminal stridulation must have been present in the common ancestor of the Ensifera ever since divergence from cockroaches." He also concluded that "tegminial stridulation became acoustically effective as a side effect of communicative vibrations and established the selective context for the later appearance of auditory function in proprioceptive tibial organs." Stridulating structures and stridulation in the Blattaria have been found definitely only in the highly evolved ovoviviparous Blaberidae (Oxyhaloinae and Panchlorinae) and they are probably late acquisitions. In Ensifera tegminal stridulation, both tegmina rub against each other to produce sound. In cockroaches, the mechanism differs in that the pronotum rubs against the tegmina.

Haskell (1955) showed that some of the energy resulting from stridulation by a grasshopper passes through the substrate either as acoustic energy or energy resulting from vibration of the body at the time of stridulation. Considerable energy is directed toward the substrate by a stridulating *N. cinerea* male (Fig. 14). No known auditory organs, like those found in the Ensifera, have been described in cockroaches. *Blattella germanica* has subgenual organs in the tibia of each leg (Graber 1882), and Autrum (1963) showed that similar organs in *Periplaneta americana* (L.) are extremely sensitive to substrate vibration. It is likely that *N. cinerea* and other stridulating cockroaches can detect sounds in this manner. Pumphrey (1940) suggested that tibial chordotonal organs developed as receptors for vibratory stimuli transmitted through the substrate, before the evolution of a tympanic membrane rendered them sensitive to air-borne sounds.

Our ideas concerning the functional significance of sound production by cockroaches are based upon laboratory observations. Field observations are unknown and are sorely needed to complete our understanding of this phenomenon.

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